



Range expansion of the invasive Tropical House Gecko, *Hemidactylus mabouia* (Squamata: Gekkonidae), in South America

^{1,*}Rudolf von May, ^{2,3}Pablo J. Venegas, ^{2,3}Germán Chávez, and ⁴Gabriel C. Costa

¹Biology Program, California State University Channel Islands, One University Drive, Camarillo, California 93012, USA ²Instituto Peruano de Herpetología, Lima, PERU ³División de Herpetología-Centro de Ornitología y Biodiversidad (CORBIDI), Santa Rita N°105 Of. 202, Urb. Huertos de San Antonio, Surco, Lima, PERU ⁴Department of Biology and Environmental Sciences, Auburn University at Montgomery, Montgomery, Alabama 36117, USA

Abstract.—This report presents new and updated distributional data of the Tropical House Gecko, *Hemidactylus mabouia*, in South America, based on 17 specimens collected between 2008 and 2019 at several localities in Peru. The updated distributional data presented here, based on georeferenced records, suggests that *H. mabouia* has experienced a geographic range expansion in northwestern South America. Additionally, we infer the origin of one of the recently established populations in central Peru by comparing mitochondrial DNA sequences with sequences from individuals of *H. mabouia* collected within the native range of the species.

Keywords. Biological invasion, *Hemidactylus frenatus*, mitochondrial DNA sequences, Peru, Reptilia

Citation: von May R, Venegas PJ, Chávez G, Costa GC. 2021. Range expansion of the invasive Tropical House Gecko, *Hemidactylus mabouia* (Squamata: Gekkonidae), in South America. *Amphibian & Reptile Conservation* 15(2) [General Section]: 323–334 (e297).

Copyright: © 2021 von May et al. This is an open access article distributed under the terms of the Creative Commons Attribution License [Attribution 4.0 International (CC BY 4.0): <https://creativecommons.org/licenses/by/4.0/>], which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. The official and authorized publication credit sources, which will be duly enforced, are as follows: official journal title *Amphibian & Reptile Conservation*; official journal website: amphibian-reptile-conservation.org.

Accepted: 1 August 2021; **Published:** 25 December 2021

Introduction

The genus *Hemidactylus* (Squamata: Gekkonidae) contains several species of widely distributed geckos that have invaded tropical and subtropical regions in the Americas over the past century (Carranza and Arnold 2006). Of these, the Tropical House Gecko, *Hemidactylus mabouia*, occurs in 12 South American countries (Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Suriname, Uruguay, and Venezuela), while the Asian House Gecko, *Hemidactylus frenatus*, only occurs in three South American countries (Colombia, Ecuador, and Venezuela) (Baldo et al. 2008; Rödder et al. 2008; Carvajal-Campos and Torres-Carvajal 2010; Torres-Carvajal 2015; Scrocchi et al. 2019). Updated distributional data from Ecuador and Colombia suggest that *H. frenatus* has experienced a recent range expansion in northwestern South America (Torres-Carvajal 2015). Additionally, new reports from Argentina suggest that *H. mabouia* has expanded its distribution into the dry Chaco (a biogeographic region that is part of the Gran Chaco Sudamericano) in recent decades (Torres et al. 2018). However, knowledge of the distribution of *H. mabouia* in the western portion of

South America remains limited. The establishment of *H. mabouia* in new areas may pose a threat to the long-term survival of native species of geckos. For example, recent studies in the Caribbean islands of Curaçao and Bonaire indicate that *H. mabouia* can effectively displace native gecko populations (*Phyllodactylus martini* and *Gonatodes antillensis*; Hughes et al. 2015).

Here, we present new and updated distributional data of *H. mabouia* in western South America, based on voucher specimens collected at several localities in Peru. All records were opportunistic and the survey effort varied across areas. All specimens were collected in human-made structures located in different settings, ranging from urban to rural to remote environments. Additionally, we infer the origin of one of the recently established populations in central Peru by comparing mitochondrial DNA sequences with sequences from individuals of *H. mabouia* collected within the native range of the species.

Materials and Methods

Specimens. This report is based on 17 specimens of *H. mabouia* collected between 2008 and 2019 at several

Correspondence. *rudolf.vonmay@csuci.edu, ORCID ID: orcid.org/0000-0003-3981-2615

Table 1. Voucher numbers, measurements, age/sex, locality, and elevation data for 17 specimens of *Hemidactylus mabouia* collected between 2008 and 2019 in Peru. SVL = Snout-Vent Length; TL = Tail Length. Latitude and longitude (in decimal degrees) and additional locality data are provided in Appendix I.

Voucher number	SVL (mm)	TL (mm)	Age/sex	Elevation (m)	Locality (all in Peru)	Year
CORBIDI 1161	31.39	29.98	Juvenile	160	San Jacinto, Loreto	2008
CORBIDI 1825	41.44	–	Juvenile	1,000	Santa Rosa de la Yunga, Cajamarca	2008
CORBIDI 3436	62.24	72.37	Male	844	Bajo Naranjillo, San Martín	2008
CORBIDI 3437	59.18	62.62	Male	844	Bajo Naranjillo, San Martín	2008
CORBIDI 3438	58.78	56.87	Female	844	Bajo Naranjillo, San Martín	2008
CORBIDI 3439	59.91	63.56	Male	844	Bajo Naranjillo, San Martín	2008
CORBIDI 3440	57.59	67.77	Female	844	Bajo Naranjillo, San Martín	2008
CORBIDI 6276	67.01	84.31	Male	140	Jenaro Herrera, Loreto	2008
CORBIDI 9030	54.29	48.66	Male	764	Tingo María, Huánuco	2011
CORBIDI 9031	55.64	72.11	Male	764	Tingo María, Huánuco	2011
MUSM 33241	55.41	69.8	Female	830	Chanchamayo, Junín	2014
CORBIDI 15363	40.31	46.25	Juvenile	123	Surquillo, Lima	2015
CORBIDI 19897	25.27	29.02	Juvenile	183	Puerto Maldonado, Madre de Dios	2016
CORBIDI 19899	21.82	16.71	Juvenile	890	Portillo Alto, Satipo, Junín	2016
CORBIDI 18738	50.29	65.11	Female	704	Chaclacayo, Lima	2018
CORBIDI 19274	62.13	60.73	Female	350	Tambopata, Madre de Dios	2018
CORBIDI 21678	63.01	–	Male	1,332	San Antonio, Satipo, Junín	2019

localities in Peru (Table 1). To verify the identity of these specimens, they were compared with specimens of both *H. mabouia* and *H. frenatus* collected within their native range and deposited in the Museum of Vertebrate Zoology (MVZ) at the University of California, Berkeley. Additionally, we photographed an adult female *H. frenatus* (MVZ 73664) collected in Bataan Province, Philippines, and one specimen of *H. mabouia* collected in Chanchamayo Province, central Peru (MUSM 33241), to illustrate differences in the external morphology between the two species. Images of live individuals in the field are provided to further illustrate these differences.

Genetic data. The genetic similarity between the specimen collected in central Peru and specimens collected in other regions were also examined. This analysis included comparing the 16S rRNA mitochondrial fragment of our sample with the sequences from other species of *Hemidactylus* (Table 2). To select sequences for comparison, we conducted a BLAST search for the 16S rRNA fragment and retrieved additional sequences from GenBank based on recent studies focusing on *Hemidactylus* geckos (Rocha et al. 2005; Carranza and Arnold 2006; Rocha et al. 2010; Rato et al. 2012; Torres-Carvajal 2015). The DNA from one specimen of *H. mabouia* from central Peru (MUSM 33241) was amplified and a phylogenetic analysis was conducted to verify its species identity.

To amplify the 16S mitochondrial fragment, the 16SA (= MVZ117; forward) primer (5'-3' sequence: CGCCTGTTTATCAAAAACAT) and the 16SB (=

MVZ98; reverse) primer (5'-3' sequence: CCGGTCTG-AACTCAGATCACGT) (Palumbi et al. 1991) were used, with the following thermocycling conditions for the Polymerase Chain Reaction (PCR): 1 cycle of 96 °C for 3 min; 35 cycles of 95 °C for 30 s, 55 °C for 45 s, 72 °C for 1.5 min; and 1 cycle of 72 °C for 7 min. The cycle sequencing reactions were completed by using the corresponding PCR primers and the BigDye Terminator 3.1 (Applied Biosystems), and sequence data were obtained by running the purified reaction products in an ABI 3730 Sequence Analyzer (Applied Biosystems). The newly obtained sequence was deposited in GenBank (Table 2). Geneious R6, version 6.1.8 (Biomatters 2013; <http://www.geneious.com/>) was used to align the sequences using the Geneious multiple alignment program for nucleotide (consensus) sequences and to obtain a Neighbor Joining tree.

A Bayesian approach was applied to infer the relatedness between our sample and those from other regions. For this purpose, MrBayes, version 3.2.0 (Ronquist and Huelsenbeck 2003) was used to infer a molecular phylogeny. The analysis included 45 terminals and a 474 bp alignment. *Tarentola angustimentalis* was used as outgroup following previous analyses focusing on *Hemidactylus* (Carranza and Arnold 2006). Before conducting the phylogenetic analysis, PartitionFinder, version 1.1.1 (Lanfear et al. 2012) was used to select the appropriate models of nucleotide evolution, and the Bayesian Information Criterion (BIC) was used to determine the best substitution model. The GTR + Γ model of nucleotide substitution (as suggested by

Table 2. GenBank accession numbers for taxa sampled in this study. The GenBank accession code of the new sequence is highlighted in bold font.

Species	16S Accession	Voucher	Locality	Reference
<i>H. frenatus</i>	AY517564	MVTIC-k27	India: Port Blair, Andaman Islands	Vences et al. 2004
<i>H. frenatus</i>	AY517561	Masc.33	Mascarenes: Cotton Bay	Rocha et al. 2005
<i>H. frenatus</i>	HM192642	MA13	Seychelles: Mahe Island, Beau Vallon	Rocha et al. 2010
<i>H. frenatus</i>	HM192643	38722	Seychelles: Mahe Island, Mont Fleuri	Rocha et al. 2010
<i>H. frenatus</i>	HM192674	DR6	Seychelles: Amirantes, Descroches	Rocha et al. 2010
<i>H. frenatus</i>	HM192677	GC1	Grand Comore: Moroni	Rocha et al. 2010
<i>H. frenatus</i>	HM192679	CAS232885	Myanmar	Rocha et al. 2010
<i>H. frenatus</i>	HM192680	CAS235221	Myanmar	Rocha et al. 2010
<i>H. mabouia</i>	OL958452	MUSM-33241	Peru: Junín, Chanchamayo	This study
<i>H. mabouia</i>	HM192552	SA31	South Africa: Port Shepstone	Rocha et al. 2010
<i>H. mabouia</i>	HM192553	SA32	South Africa: Port Shepstone	Rocha et al. 2010
<i>H. mabouia</i>	HM192554	SA33	South Africa: Port Shepstone	Rocha et al. 2010
<i>H. mabouia</i>	HM192555	SA30	South Africa: Port Shepstone	Rocha et al. 2010
<i>H. mabouia</i>	HM192557	Z1	Tanzania: Zanzibar Inland, Stone Town	Rocha et al. 2010
<i>H. mabouia</i>	HM192558	Z40	Tanzania: Zanzibar Inland, Upenja	Rocha et al. 2010
<i>H. mabouia</i>	HM192559	PB5	Tanzania: Pemba Inland, Mkoani	Rocha et al. 2010
<i>H. mabouia</i>	HM192560	TZ6	Tanzania: Dar Es Salaam	Rocha et al. 2010
<i>H. mabouia</i>	HM192561	Z19	Tanzania: Zanzibar Inland, Chwaka	Rocha et al. 2010
<i>H. mabouia</i>	HM192601	SA21	South Africa: Durban	Rocha et al. 2010
<i>H. mabouia</i>	HM192602	SA22	South Africa: Durban	Rocha et al. 2010
<i>H. mabouia</i>	HM192603	SA18	South Africa: Durban	Rocha et al. 2010
<i>H. mabouia</i>	HM192604	SA34	South Africa: Port Elizabeth	Rocha et al. 2010
<i>H. mabouia</i>	HM192605	SA19	South Africa: Durban	Rocha et al. 2010
<i>H. mabouia</i>	HM192606	SA23	South Africa: Durban	Rocha et al. 2010
<i>H. mabouia</i>	HM192607	SA27	South Africa: Port Shepstone	Rocha et al. 2010
<i>H. mabouia</i>	HM192608	SA28	South Africa: Port Shepstone	Rocha et al. 2010
<i>H. mabouia</i>	HM192609	SA29	South Africa: Port Shepstone	Rocha et al. 2010
<i>H. mabouia</i>	JF329705	3MA39	Seychelles: Mahe Island, Baie Lazare	Rocha et al. 2010
<i>H. mabouia</i>	JF329706	3MA41	Seychelles: Mahe Island, Baie Lazare	Rocha et al. 2010
<i>H. platycephalus</i>	AY517571	GC33	Grand Comore: Itsoundzou	Vences et al. 2004
<i>H. platycephalus</i>	AY517572	Mozamb_e01	Mozambique: Zambezia	Vences et al. 2004
<i>H. platycephalus</i>	AY517573	MtSambaro_2000e64_k44	Mayotte: Chissioua Mtsamboro	Vences et al. 2004
<i>H. platycephalus</i>	AY517574	NB_2000c22_k40	Madagascar: Nosy Be	Vences et al. 2004
<i>Tarentola angustimentalis</i>	JQ301000	DB1402	Spain: Lanzarote	Rato et al. 2012
<i>Tarentola boehmei</i>	JQ300878	DB241	Morocco: Akka Ighane	Rato et al. 2012

PartitionFinder) was used to perform an MCMC Bayesian analysis that consisted of two simultaneous runs of 8,000,000 generations, and the sampling rate was set to once every 1,000 generations. Each run had three heated chains and one “cold” chain, and the burn-in was set to discard the first 25% samples from the cold chain. At the end of the run, the average standard deviation of split frequencies was 0.004405. Following the completion of the analysis, Tracer 1.6 (Rambaut and Drummond 2003) was used to verify convergence. Subsequently, FigTree (<http://tree.bio.ed.ac.uk/software/figtree/>) was used to visualize the majority-rule consensus tree and the posterior probability values to assess node support.

Additionally, the R package APE (Paradis et al. 2004) was used to estimate uncorrected *p*-distances (i.e., the proportion of nucleotide sites at which any two sequences are different).

Mapping. The occurrence of *H. mabouia* in South America was mapped using georeferenced data from previous studies (Kluge 1969; Dirksen and De la Riva 1999; Lehr 2001; Baldo et al. 2008; Rödder et al. 2008; Carvajal-Campos and Torres-Carvajal 2010; Diele-Viegas et al. 2018; Torres et al. 2018; Caicedo-Portilla 2019; Scrocchi et al. 2019) and this study. Additionally, 656 georeferenced records available in

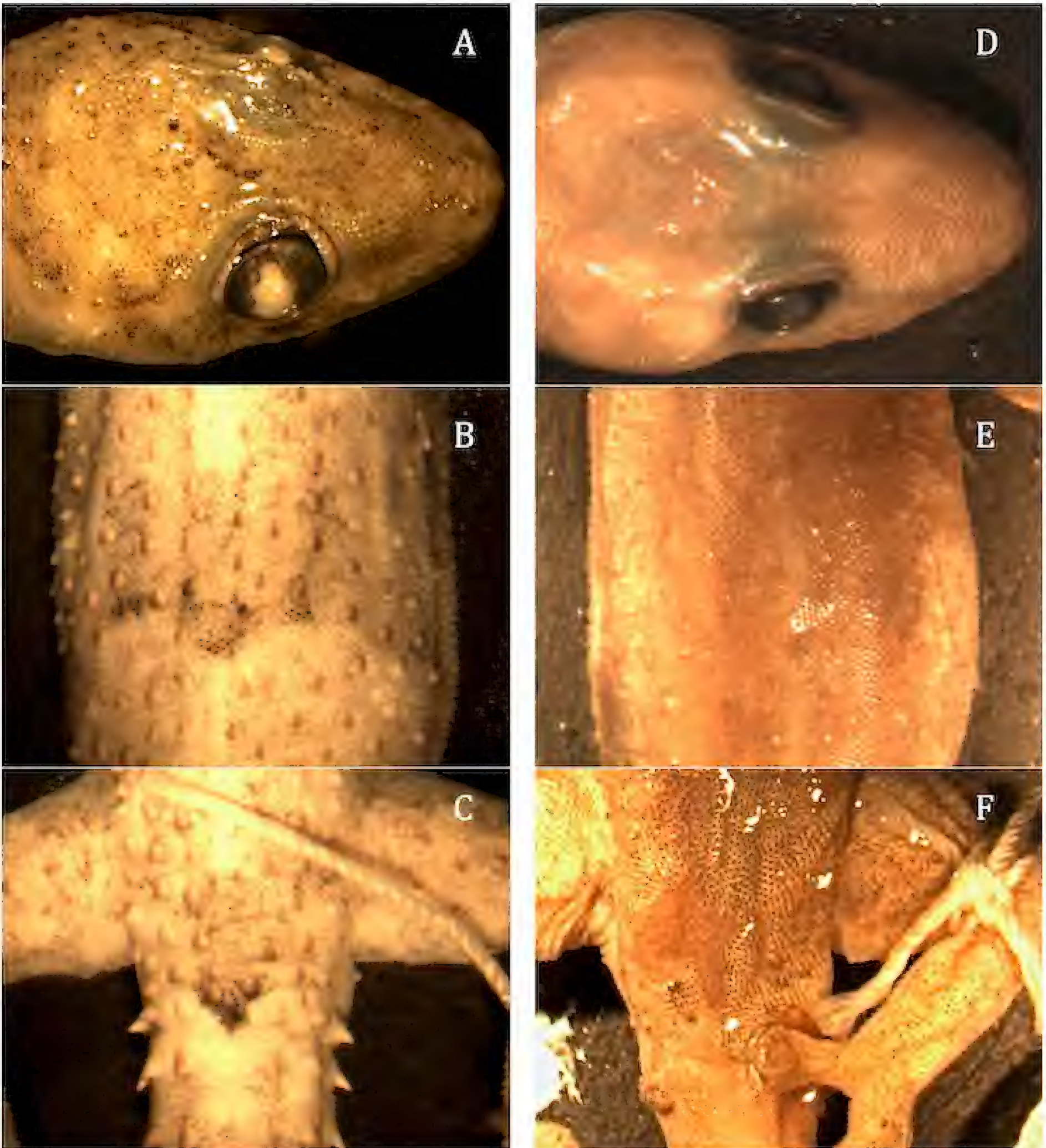


Fig. 1. Dorsal views of head (A), midbody (B), and tail (C) of adult female of *Hemidactylus mabouia* (MUSM 33241; Field Nbr. RvM64–14) collected in Chanchamayo, Peru. Dorsal views of head (D), midbody (E), and tail (F) of adult female *Hemidactylus frenatus* (MVZ 73664) collected in Bataan Province, Philippines. Photographs by Rudolf von May.

the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org>) were included. Only those GBIF records with voucher specimen data were included and those that lacked specimen data (e.g., iNaturalist photo records) or had inaccurate coordinate data (i.e., coordinate uncertainty > 3,000 m) were excluded. The R package *maptools* (Bivand and Lewin-Koh 2014) was used to produce a map depicting the known occurrence points of *H. mabouia*. A layer depicting the Global Biomes according to the World Wildlife Fund (WWF)

classification, obtained from the Terrestrial Ecoregions of the World dataset (WWF 2008), was also incorporated to determine the primary ecoregions used by this species.

Results

The morphology of all specimens listed in Table 1 closely matches *H. mabouia* and differs from *H. frenatus* (Figs. 1–2). Dorsal conical tubercles are higher in our specimens as well as *H. mabouia* from Africa. This

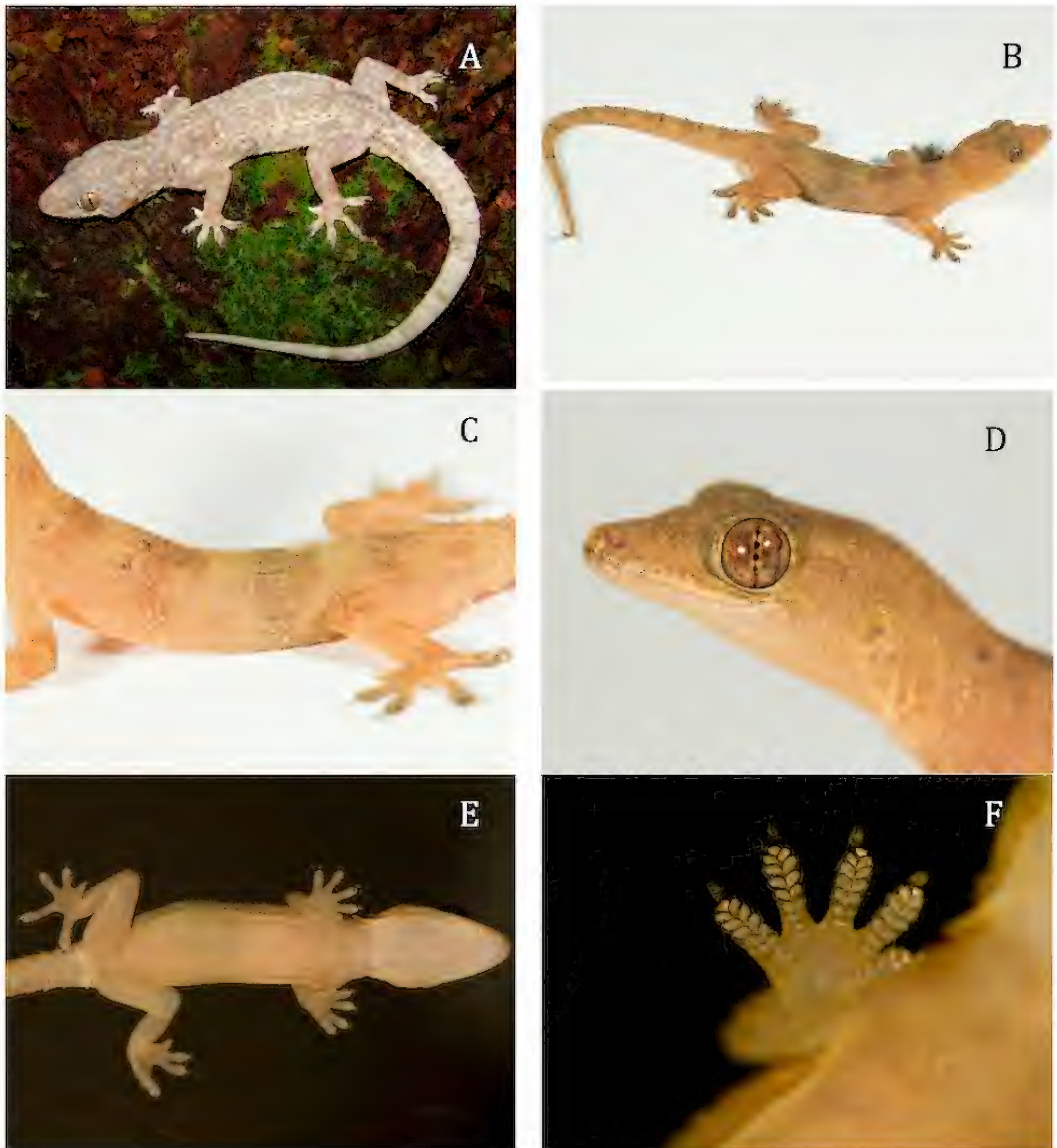


Fig. 2. Dorsal views of adult male *Hemidactylus mabouia* (CORBIDI 6276) collected in Loreto (Genaro Herrera, Requena Province), Peru (A). Dorsal view of juvenile *Hemidactylus mabouia* (CORBIDI 15363) collected in Lima (Surquillo, Lima Province), Peru (B). Lateral view of body (C) and head (D), ventral view of head and body (E), and ventral view of right hand (F) of the same individual (CORBIDI 15363). Photographs by Pablo Venegas (A) and Germán Chávez (B–F).

character is notoriously different in *H. frenatus* (lower dorsal tubercles), which is also evident in Figs. 1–3. The specimens reported here were collected in seven regions in Peru (from north to south): Loreto, Cajamarca, San Martín, Huánuco, Junín, Lima, and Madre de Dios. One of the specimens collected in Lima (CORBIDI 15363) was found in a house wall close to a city park in Surquillo district, a dense urban area, at 123 m elevation. The other specimen collected in Lima (CORBIDI 18738) was found

in a backyard in Chaclacayo district, an urban area, at an elevation of 704 m. This specimen was captured on a wall with a small collection of orchids brought from Tarapoto and Moyobamba. One of the specimens found in Madre de Dios (CORBIDI 19274) was captured on a wooden wall at the Tambopata Research Center, a research station and ecotourism lodge located in the Tambopata National Reserve. All other specimens (including the specimen from Lima) were collected outside of natural



Fig. 3. Dorsolateral views of adult *Hemidactylus frenatus* from Aur Island, Malaysia (A), Nam Du Island, Vietnam (B), and Villavicencio, Meta, Colombia (C–D). Photographs by L. Lee Grismer (A–B) and Juan D. Vásquez-Restrepo (C–D).

protected areas. The phylogenetic analysis focusing on the 16S rRNA gene (Fig. 4) indicated that the haplotype of the specimen collected in Junín region, central Peru, is identical to the haplotype of specimens of *H. mabouia* from Annodon Island, West Africa, and the Republic of South Africa. Uncorrected *p*-distances are shown in Appendix II. Although several terminals in the *H. mabouia* clade are labeled as *H. mercatorius*, we believe they represent *H. mabouia*. This apparent discrepancy appears because we retained the original species assignment provided in GenBank.

The geographic distribution of *H. mabouia* in South America includes 12 countries (Fig. 5). The new records from Peru are based on field observations and voucher specimens collected between 2008 and 2019 (Table 1). Other relatively recent records in Peru (1989–1999) are from San Martín (KU 212605–212609; <https://www.gbif.org>) and Huánuco regions (SMF 80088; Lehr 2001). Our records from Lima are among the first observations of *H. mabouia* west of the Andes, in addition to recent records from coastal Ecuador (Carvajal-Campos and Torres-Carvajal 2010).

Discussion

The findings of this study suggest that *H. mabouia* has recently expanded its geographic distribution in western South America. Previous studies had documented the presence of *H. mabouia* in western Ecuador and

Colombia (Rödder et al. 2008; Carvajal-Campos and Torres-Carvajal 2010; Caicedo-Portilla 2019), and previous records from Peru were obtained in lowland Amazonian sites located at or below 200 m of elevation (Kluge 1969; Carrillo and Icochea 1995; Lehr 2001; Rödder et al. 2008; Cossios 2010). Our locality data represent a notable extension (> 330 km to the west and > 600 km to the southeast) of the known geographic range of *H. mabouia* in Peru. Additionally, our data suggest that there has been a recent expansion of *H. mabouia* into tropical montane forests in Peru. *Hemidactylus mabouia* was found at lowland sites close to the Peruvian Andes in 1989 and 1999 (Fig. 5), and it was first noticed in montane forest (Chanchamayo, Selva Central) in 2005 (R. von May, Pers. Obs.). Subsequently, specimens were collected at six montane forest sites in both central and northern Peru between 2008 and 2019 (Table 1). These records extend the elevational distribution in Peru by over 1,100 m. As a result, the elevational distribution of *H. mabouia* in Peru ranges from 140 to 1,332 m.

The phylogenetic analysis focusing on the 16S rRNA gene (Fig. 5, Table 4) indicated that the haplotype of one population of *H. mabouia* surveyed in central Peru is identical to that of populations of *H. mabouia* from São Tomé and Príncipe Island and Annodon Island (Gulf of Guinea, West Africa), as well as populations from the Republic of South Africa (Rocha et al. 2005; Rocha et al. 2010). When considering the high similarity between *H. mabouia* and *H. mercatorius*, Rocha et al.

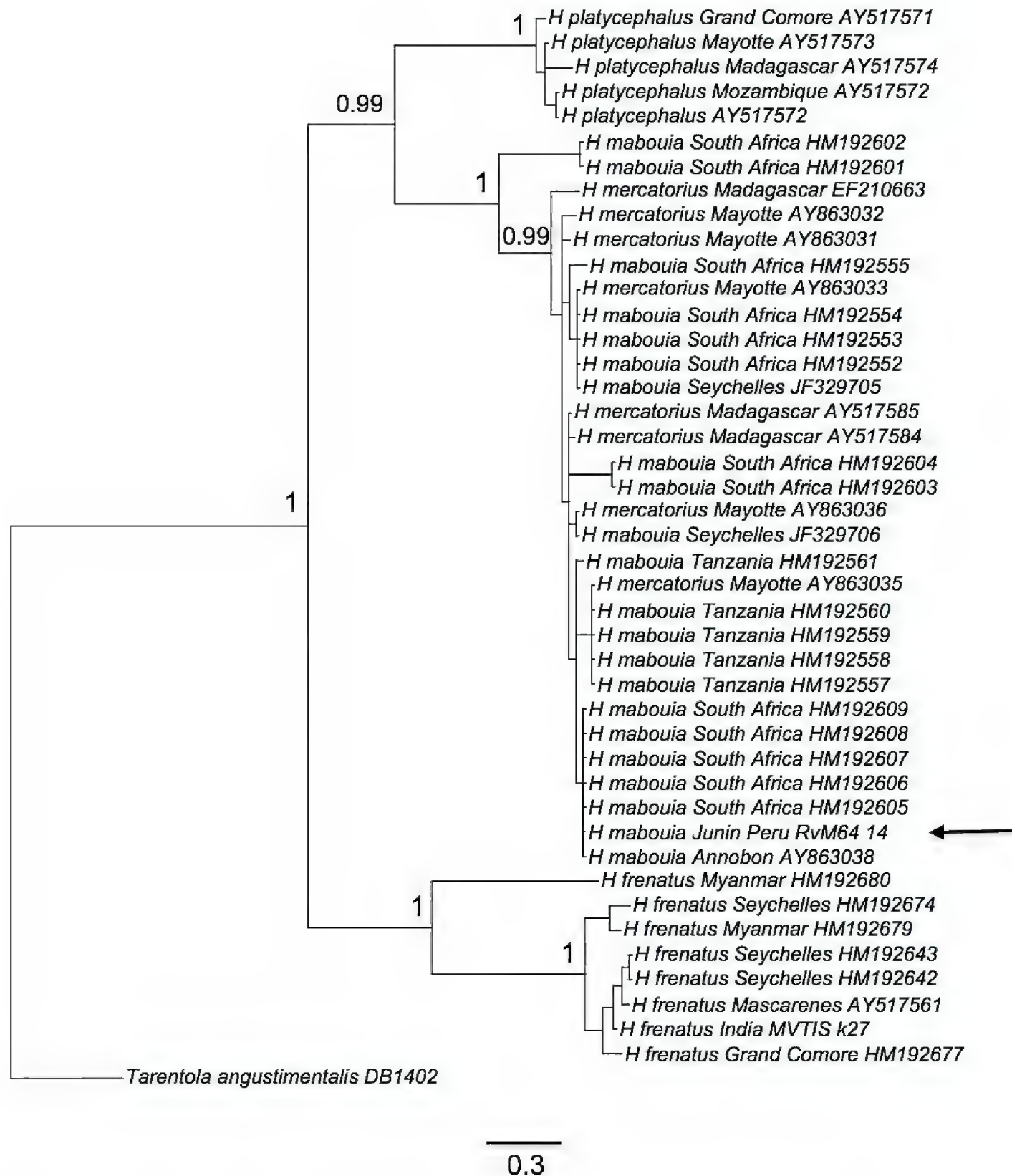


Fig. 4. A consensus Bayesian phylogeny based on 474 bp of aligned mitochondrial sequences (16S rRNA gene). Posterior probability values are shown on nodes. The arrow indicates the specimen from central Peru (MUSM 33241; Field Nbr. RvM64–14).

(2005) mentioned the possibility of a “species complex” encompassing taxa currently identified under either of these two names. Vences et al. (2004) also proposed that the Malagasy populations of *H. mabouia* should be recognized as *H. mercatorius*. Furthermore, Rocha et al. (2010) identified multiple cryptic lineages within this *H. mercatorius-mabouia* species complex and proposed that insular populations of *H. mabouia* off the coasts of western and eastern Africa (Gulf of Guinea, Comoros, Madagascar, and Seychelles) should be recognized as *H. mercatorius*, while the status of continental populations required further studies. Accordingly, recent IUCN conservation status assessments followed Rocha et al. (2010) and restricted the name *H. mercatorius* to island populations within the *H. mercatorius-mabouia* clade (Vences and Hawlitschek 2011). As a result, the continental populations will continue to be recognized as *H. mabouia* until the taxonomy of this species complex

is resolved. Thus, given that the specimen we collected in central Peru has mitochondrial sequences that are identical to *H. mabouia* from the Republic of South Africa, we consider that this and all other (morphologically similar) specimens collected in Peru represent *H. mabouia*.

The specimens of *H. mabouia* collected in Lima are noteworthy because they represent the first records of this species in the Pacific coastal desert, the driest ecoregion in Peru (Brack 1986). These records are among the first observations of *H. mabouia* west of the Andes, in addition to records from coastal Ecuador (Carvajal-Campos and Torres-Carvajal 2010). How this species arrived in Lima remains unknown, but its arrival on the Peruvian coast might have occurred as a stowaway through the Pacific Ocean or via terrestrial or aerial domestic journeys. Lima is located near Callao, the main maritime port in the country, and it is also the main hub for bus routes and both domestic and international flights. Human-mediated

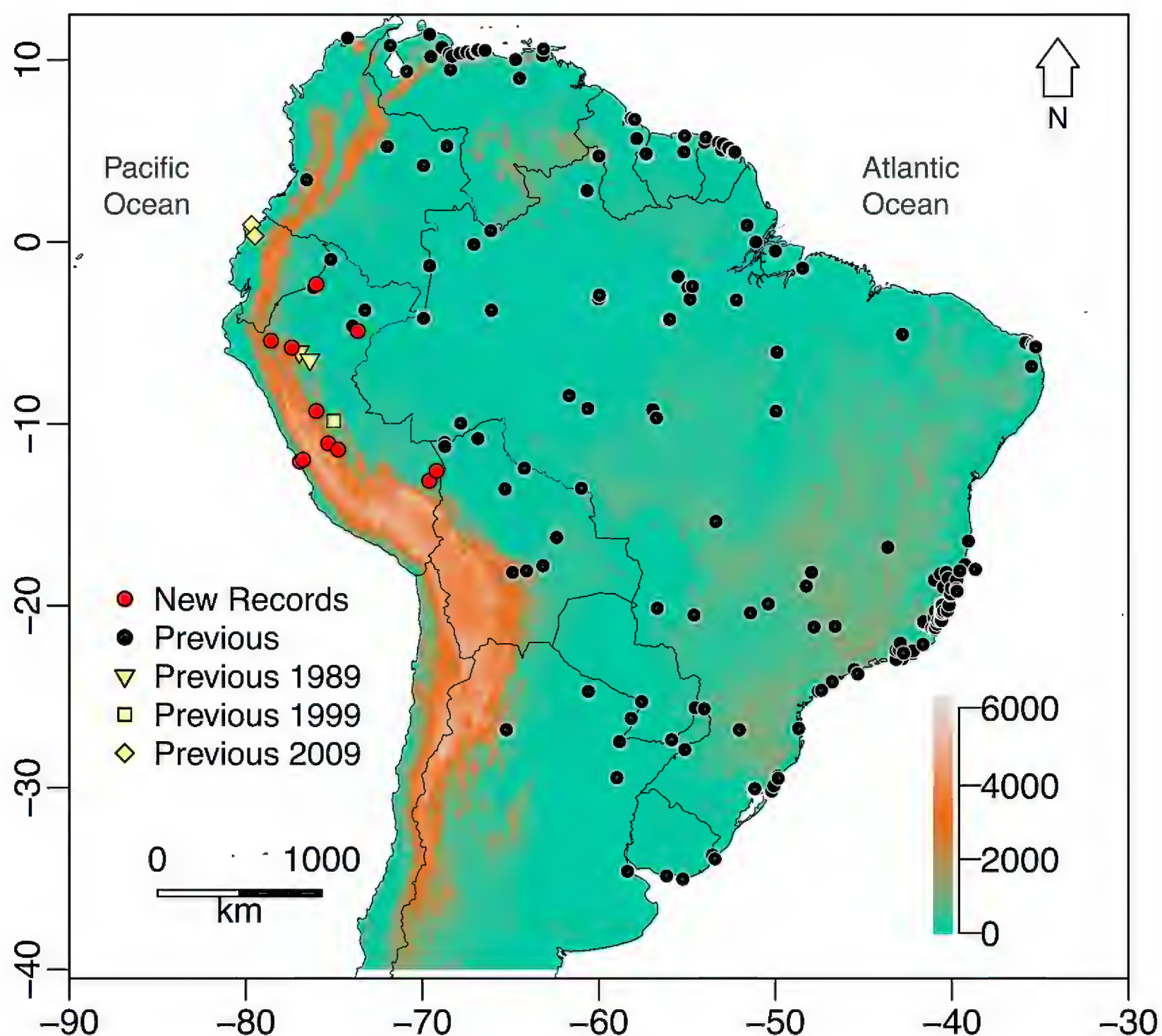


Fig. 5. Known distribution of *Hemidactylus mabouia* in South America. Black circles represent literature data (most previous records) and red circles indicate the location of new records in Peru (2008–2019). Other relatively recent records in Peru (1989–1999) are from the San Martín and Huánuco regions (yellow triangle and square). Recent records from coastal Ecuador are indicated with yellow diamonds. The color scheme of the map represents the elevation in m asl (see legend on the right).

dispersal in combination with favorable anthropogenic habitats will facilitate the establishment of this gecko in Lima and other cities along the west coast of tropical South America (Colombia, Ecuador, Peru, and northern Chile).

Our finding of *H. mabouia* at the Tambopata Research Center (Madre de Dios region) represents the first record of this invasive species in a natural protected area in Peru, the Tambopata National Reserve. As for the other specimens reported here, the occurrence of this population might be restricted to human-made buildings, but not forests. Our survey efforts (~7 person-days) did not yield any records of this species in the lowland rainforest surrounding the station. In contrast, we were able to observe several individuals on walls or behind furniture of the Tambopata Research Center. Boats transporting people and supplies from Puerto Maldonado, the nearest city (where we also recorded *H. mabouia*; Table 1), frequently arrive at this and other lodges and hotels located in the reserve. Thus, given that boats are the primary transportation method to these lodges and considering that this gecko can easily

travel as a stowaway in boats, it is likely that *H. mabouia* is currently present in many other lowland rainforest sites with human-made buildings. Yet, the impact of *H. mabouia* on the native fauna remains unclear. For example, the nocturnal gecko *Thecadactylus solimoensis* is also present in the region (Doan and Arizabal Arriaga 2002; von May et al. 2009), occasionally uses the same type of habitats and may compete for resources such as food, retreat, and nesting sites.

We believe that the new data presented here lend support to the hypothesis that *H. mabouia* has recently expanded its geographic distribution in western South America. This is because *H. mabouia* had not previously been recorded at sites that were subject to intensive herpetological surveys in previous decades (e.g., Tambopata Research Center; Doan and Arizabal Arriaga 2002) but was recorded in the most recent decade (this study). Likewise, two of the authors (PJV, GC) have worked in Lima and other coastal areas since the late 1990s, but only recently recorded *H. mabouia* on the Peruvian Pacific coast (this study). While some of the

sites reported here had been visited multiple times by herpetologists, it is possible that *H. mabouia* is more common than previously thought. Additional surveys will provide relative abundance data for this invasive species, and future studies need to test whether *H. mabouia* can displace native gecko populations.

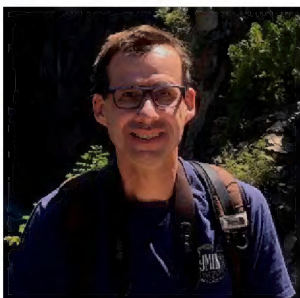
Acknowledgments.—We thank Juan Carlos Chávez-Arribasplata, Amanda Delgado, Lizet Tejada, Jorge Reto, Eduardo Almora, Napoleón Monsalve, Luis García, Jesús Ormeño, and Axel Marchelie for help with data collection. We thank L. Lee Grismer and Juan D. Vásquez-Restrepo for sharing images of *H. frenatus* photographed in the field. We thank Dennis Rödder and GBIF for kindly providing some of the georeferenced data used in this study. Research and collecting permits were approved by the Dirección General Forestal y de Fauna Silvestre (DGFFS), Servicio Nacional Forestal y de Fauna Silvestre, and the Ministry of Agriculture (09 C/C-2008-INRENA-IANP, 120-2012-AG-DGFFS-DGEFFS, 064-2013-AG-DGFFS-DGEFFS, 292-2014-AG-DGFFS-DGEFFS, and Contrato de Acceso Marco a Recursos Genéticos N° 359-2013-MINAGRI-DGFFS-DGEFFS). We thank Claudia Koch and one anonymous reviewer for providing constructive comments on the manuscript. This research was supported with grants from the National Science Foundation (Postdoctoral Research Fellowship DBI-1103087) and the National Geographic Society (Grant # 9191-12) to RvM. GCC was supported by NSF grant DEB-1754425.

Literature Cited

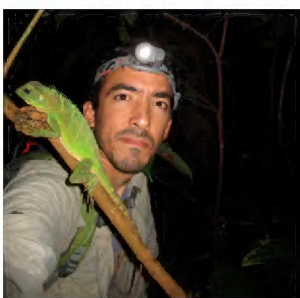
- Baldo D, Bortiero C, Brusquetti F, García JE, Prigioni C. 2008. Notes on geographic distribution: Reptilia, Gekkonidae, *Hemidactylus mabouia*, *Tarentola mauritanica*: distribution extension and anthropogenic dispersal. *Check List* 4: 434–438.
- Bivand R, Lewin-Koh N. 2014. maptools: tools for reading and handling spatial objects. – R package ver. 0.8–30. Available: <https://cran.r-project.org/package=maptools> [Accessed: 17 January 2021].
- Brack A. 1986. Ecología de un país Complejo. Pp. 175–319 In: *Gran Geografía del Perú*. Editors, Dourojeanni MJ, Mejía Baca J. Naturaleza y Hombre, Barcelona, Spain.
- Caicedo-Portilla JR. 2019. Presencia de *Hemidactylus frenatus* y *Hemidactylus mabouia* (Squamata: Gekkonidae) en Leticia, Amazonía colombiana. *Biota Colombiana* 20(2): 120–127.
- Carranza S, Arnold EN. 2006. Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 38: 531–545.
- Carrillo N, Icochea J. 1995. Lista taxonómica preliminar de los reptiles vivientes del Perú. *Publicaciones del Museo de Historia Natural Universidad Nacional de San Marcos. Serie A Zoología* 49: 1–27.
- Carvajal-Campos A, Torres-Carvajal O. 2010. *Hemidactylus mabouia* Moreau De Jonnés, 1818 and *H. frenatus* Schlegel, 1836 in western Ecuador: new records reveal range extension. *Herpetozoa* 23: 90–91.
- Cossios ED. 2010. Vertebrados naturalizados en el Perú: historia y estado del conocimiento. *Revista Peruana de Biología* 17(2): 179–189.
- Diele-Viegas LM, Vitt LJ, Sinervo B, Colli GR, Werneck FP, Miles DB, Magnusson WE, Santos JC, Sette CM, Caetano GHO, et al. 2018. Thermal physiology of Amazonian lizards (Reptilia: Squamata). *PLoS ONE* 13(3): e0192834.
- Dirksen L, De la Riva I. 1999. The lizards and amphisbaenians of Bolivia (Reptilia, Squamata): checklist, localities, and bibliography. *Graellsia* 55: 199–215.
- Doan TM, Arizabal Arriaga W. 2002. Microgeographic variation in species composition of the herpetofaunal communities of Tambopata Region, Peru. *Biotropica* 34: 101–117.
- Hughes DF, Meshaka WE, Van Buurt G. 2015. The superior colonizing gecko *Hemidactylus mabouia* on Curacao: conservation implications for the native gecko *Phyllodactylus martini*. *Journal of Herpetology* 49(1): 60–63.
- Kluge AG. 1969. The evolution and geographical origin of the New World *Hemidactylus mabouia-brooki* complex (Gekkonidae, Sauria). *Miscellaneous Publications of the Museum of Zoology, University of Michigan* 138: 1–78.
- Lanfear R, Calcott B, Ho SYW, Guindon S. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29: 1,695–1,701.
- Lehr E. 2001. New records for amphibians and reptiles from Departamentos Pasco and Ucayali, Peru. *Herpetological Review* 32(2): 130–132.
- Palumbi SR, Martin A, Romano S, McMillan WO, Stice L, Grabawski G. 1991. *The Simple Fool's Guide to PCR, Version 2.0*. Privately published, compiled by S. Palumbi, University of Hawaii, Honolulu, Hawaii, USA. 45 p.
- Paradis E, Claude J, Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20(2): 289–290.
- Rambaut A, Drummond, A. 2003. Tracer: a program for analyzing results from Bayesian MCMC programs such as BEAST and MrBayes. Available: <http://beast.bio.ed.ac.uk/Tracer> [Accessed: 18 September 2016].
- Rato C, Carranza S, Harris DJ. 2012. Evolutionary history of the genus *Tarentola* (Gekkota: Phyllodactylidae) from the Mediterranean Basin, estimated using multilocus sequence data. *BMC Evolutionary Biology*

12: 14

- Rocha S, Carretero MA, Harris DJ. 2005. Diversity and phylogenetic relationships of *Hemidactylus* geckos from the Comoro islands. *Molecular Phylogenetics and Evolution* 35(1): 292–299.
- Rocha S, Carretero MA, Harris DJ. 2010. On the diversity, colonization patterns, and status of *Hemidactylus* sp. (Reptilia: Gekkonidae) from the Western Indian Ocean islands. *Herpetological Journal* 20(2): 83–89.
- Rödter D, Solé M, Böhme W. 2008. Predicting the potential distributions of two alien invasive House Geckos (Gekkonidae: *Hemidactylus frenatus*, *Hemidactylus mabouia*). *North-Western Journal of Zoology* 4: 236–246.
- Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1,572–1,574.
- Scrocchi GJ, Stazzonelli JC, Cabrera P. 2019. Nuevas citas de Squamata (Gekkonidae, Phyllodactylidae y Dipsadidae) para la provincia de Tucumán, Argentina. *Cuadernos de Herpetología* 33(2): 75–78.
- Sound P, Kosuch J, Vences M, Seitz M, Veith M. 2006. Preliminary molecular relationships of Comoran Day Geckos (*Phelsuma*). Pp. 175–179 In: *Proceedings of the 13th Congress of the Societas Europaea Herpetologica*. SEH, Bonn, Germany. 262 p.
- Torres-Carvajal O. 2015. On the origin of South American populations of the Common House Gecko (Gekkonidae: *Hemidactylus frenatus*). *NeoBiota* 27: 69–79.
- Torres PJ, Escalante O, Cardozo D. 2018. First record of the invasive *Hemidactylus mabouia* (Moreau de Jonnés, 1818) (Squamata, Gekkonidae), in the dry Chaco, Argentina. *Check List* 14(4): 633–636.
- Vences M, Hawlitschek O. 2011. *Hemidactylus mercatorius*. The IUCN Red List of Threatened Species 2011: e.T172976A6951505.
- Vences M, Wanke S, Vieites DR, Branch B, Glaw F. 2004. Natural colonization or introduction? High genetic divergences and phylogeographic relationships of House Geckos (*Hemidactylus*) from Madagascar. *Biological Journal of the Linnean Society* 83: 115–130.
- von May R, Siu-Ting K, Jacobs JM, Medina-Müller M, Gagliardi G, Rodríguez LO, Donnelly MA. 2009. Species diversity and conservation status of amphibians in Madre de Dios, Peru. *Herpetological Conservation and Biology* 4: 14–29.
- World Wildlife Fund. 2008. Terrestrial ecoregions of the world. World Wildlife Fund (WWF), Washington, DC, USA. Available: <https://www.worldwildlife.org/biome-categories/terrestrial-ecoregions> [Accessed: 25 February 2018].



Rudolf von May is an Assistant Professor in the Biology Program at California State University Channel Islands, Camarillo, California, USA. His fields of interest include evolutionary ecology, herpetology, and biodiversity conservation.



Pablo J. Venegas is Curator of the Herpetological Collection of Centro de Ornitología y Biodiversidad (CORBIDI) and the Instituto Peruano de Herpetología, in Lima, Peru. His primary research interests include the diversity and conservation of the Neotropical herpetofauna, with an emphasis on Peru and Ecuador.



Germán Chávez is an Associated Researcher at the of Centro de Ornitología y Biodiversidad (CORBIDI) and the Instituto Peruano de Herpetología, in Lima, Peru. His primary research interests include the taxonomy and systematics of amphibians and reptiles.



Gabriel C. Costa is an Associate Professor in the Department of Biology and Environmental Sciences at Auburn University at Montgomery, Alabama, USA. His primary research interests include biogeography, macroecology, herpetology, and conservation biology.

Appendix I. Locality data, including latitude and longitude (in decimal degrees) and collection dates, of specimens reported in this study.

Species	Elevation (m)	Latitude	Longitude	Locality	Province	Year observed
<i>H. mabouia</i>	1,000	-5.43645	-78.56963	Santa Rosa de La Yunga	Jaen	2008
<i>H. mabouia</i>	844	-5.81076	-77.38919	Bajo Naranjillo	Rioja	2008
<i>H. mabouia</i>	844	-5.81076	-77.38919	Bajo Naranjillo	Rioja	2008
<i>H. mabouia</i>	844	-5.81076	-77.38919	Bajo Naranjillo	Rioja	2008
<i>H. mabouia</i>	844	-5.81076	-77.38919	Bajo Naranjillo	Rioja	2008
<i>H. mabouia</i>	844	-5.81076	-77.38919	Bajo Naranjillo	Rioja	2008
<i>H. mabouia</i>	123	-12.07814	-76.93644	Surquillo	Lima	2015
<i>H. mabouia</i>	704	-11.97099	-76.75121	Chaclacayo	Lima	2018
<i>H. mabouia</i>	764	-9.29970	-76.00040	Tingo Maria Hotel	Leoncio Prado	2011
<i>H. mabouia</i>	764	-9.29970	-76.00040	Tingo Maria Hotel	Leoncio Prado	2011
<i>H. mabouia</i>	160	-2.33083	-75.99703	San Jacinto	Loreto	2008
<i>H. mabouia</i>	830	-11.07981	-75.32844	Chunchuyacu	Chanchamayo	2014
<i>H. mabouia</i>	140	-4.89911	-73.65000	Jenaro Herrera	Requena	2008
<i>H. mabouia</i>	350	-13.13333	-69.60000	TRC	Tambopata	2018
<i>H. mabouia</i>	183	-12.59090	-69.19630	Puerto Maldonado	Tambopata	2016
<i>H. mabouia</i>	1,332	-11.41932	-74.76582	San Antonio	Satipo	2019

Hemidactylus mabouia in South America

Appendix II. Genetic distances between *H. mabouia* from Central Peru, *H. mabouia* from other regions, and related taxa. Uncorrected *p*-distances of the mitochondrial 16S rRNA gene.

	1	2	3	4	5	6	7	8	9	10
1 <i>H. frenatus</i> Grand Comore HM192677										
2 <i>H. frenatus</i> India MVTIS k27	0.013									
3 <i>H. frenatus</i> Mascarenes AY517561	0.013	0.007								
4 <i>H. frenatus</i> Myanmar HM192679	0.026	0.022	0.029							
5 <i>H. frenatus</i> Myanmar HM192680	0.126	0.128	0.126	0.128						
6 <i>H. frenatus</i> Seychelles HM192642	0.013	0.007	0.004	0.029	0.131					
7 <i>H. frenatus</i> Seychelles HM192643	0.013	0.007	0.004	0.029	0.131	0.000				
8 <i>H. frenatus</i> Seychelles HM192674	0.031	0.027	0.033	0.013	0.142	0.033	0.033			
9 <i>H. mabouia</i> Annobon AY863038	0.203	0.202	0.202	0.205	0.189	0.209	0.209	0.205		
10 <i>H. mabouia</i> Junin Peru RvM64 14	0.206	0.206	0.206	0.208	0.192	0.212	0.212	0.208	0.000	
11 <i>H. mabouia</i> Seychelles JF329705	0.220	0.220	0.220	0.226	0.213	0.227	0.227	0.223	0.012	0.012
12 <i>H. mabouia</i> Seychelles JF329706	0.213	0.212	0.212	0.219	0.209	0.219	0.219	0.215	0.007	0.007
13 <i>H. mabouia</i> South Africa HM192552	0.220	0.220	0.220	0.226	0.213	0.227	0.227	0.223	0.012	0.012
14 <i>H. mabouia</i> South Africa HM192553	0.220	0.220	0.220	0.226	0.213	0.227	0.227	0.223	0.012	0.012
15 <i>H. mabouia</i> South Africa HM192554	0.220	0.220	0.220	0.226	0.213	0.227	0.227	0.223	0.012	0.012
16 <i>H. mabouia</i> South Africa HM192555	0.218	0.218	0.218	0.224	0.216	0.225	0.225	0.221	0.017	0.017
17 <i>H. mabouia</i> South Africa HM192601	0.221	0.221	0.221	0.224	0.201	0.228	0.228	0.220	0.074	0.074
18 <i>H. mabouia</i> South Africa HM192602	0.221	0.221	0.221	0.224	0.201	0.228	0.228	0.220	0.074	0.074
19 <i>H. mabouia</i> South Africa HM192603	0.226	0.226	0.226	0.232	0.210	0.229	0.229	0.225	0.025	0.025
20 <i>H. mabouia</i> South Africa HM192604	0.226	0.226	0.226	0.232	0.210	0.229	0.229	0.225	0.025	0.025
21 <i>H. mabouia</i> South Africa HM192605	0.220	0.219	0.219	0.226	0.209	0.226	0.226	0.222	0.000	0.000
22 <i>H. mabouia</i> South Africa HM192606	0.220	0.219	0.219	0.226	0.209	0.226	0.226	0.222	0.000	0.000
23 <i>H. mabouia</i> South Africa HM192607	0.220	0.219	0.219	0.226	0.209	0.226	0.226	0.222	0.000	0.000
24 <i>H. mabouia</i> South Africa HM192608	0.220	0.219	0.219	0.226	0.209	0.226	0.226	0.222	0.000	0.000
25 <i>H. mabouia</i> South Africa HM192609	0.220	0.219	0.219	0.226	0.209	0.226	0.226	0.222	0.000	0.000
26 <i>H. mabouia</i> Tanzania HM192557	0.219	0.226	0.226	0.225	0.223	0.233	0.233	0.222	0.010	0.010
27 <i>H. mabouia</i> Tanzania HM192558	0.219	0.226	0.226	0.225	0.223	0.233	0.233	0.222	0.010	0.010
28 <i>H. mabouia</i> Tanzania HM192559	0.219	0.226	0.226	0.225	0.223	0.233	0.233	0.222	0.010	0.010
29 <i>H. mabouia</i> Tanzania HM192560	0.219	0.226	0.226	0.225	0.223	0.233	0.233	0.222	0.010	0.010
30 <i>H. mabouia</i> Tanzania HM192561	0.216	0.216	0.216	0.222	0.216	0.223	0.223	0.219	0.005	0.005
31 <i>H. mercatorius</i> Madagascar AY517584	0.203	0.203	0.203	0.205	0.192	0.209	0.209	0.205	0.006	0.006
32 <i>H. mercatorius</i> Madagascar AY517585	0.200	0.200	0.200	0.202	0.192	0.206	0.206	0.202	0.004	0.004
33 <i>H. mercatorius</i> Madagascar EF210663	0.215	0.214	0.214	0.217	0.180	0.221	0.221	0.217	0.022	0.022
34 <i>H. mercatorius</i> Mayotte AY863031	0.206	0.202	0.202	0.205	0.192	0.209	0.209	0.205	0.011	0.011
35 <i>H. mercatorius</i> Mayotte AY863032	0.203	0.203	0.203	0.205	0.186	0.209	0.209	0.205	0.013	0.013
36 <i>H. mercatorius</i> Mayotte AY863033	0.206	0.205	0.205	0.208	0.195	0.212	0.212	0.208	0.011	0.011
37 <i>H. mercatorius</i> Mayotte AY863035	0.205	0.211	0.211	0.207	0.203	0.217	0.217	0.207	0.009	0.009
38 <i>H. mercatorius</i> Mayotte AY863036	0.199	0.199	0.199	0.202	0.192	0.205	0.205	0.202	0.006	0.006
39 <i>H. platycephalus</i> AY517572	0.161	0.161	0.161	0.158	0.174	0.161	0.161	0.155	0.120	0.120
40 <i>H. platycephalus</i> Grand Comore AY517571	0.165	0.162	0.162	0.159	0.175	0.162	0.162	0.156	0.118	0.118
41 <i>H. platycephalus</i> Madagascar AY517574	0.164	0.161	0.161	0.161	0.176	0.162	0.162	0.159	0.127	0.127
42 <i>H. platycephalus</i> Mayotte AY517573	0.167	0.164	0.164	0.158	0.177	0.164	0.164	0.155	0.117	0.117
43 <i>H. platycephalus</i> Mozambique AY517572	0.161	0.161	0.161	0.158	0.174	0.161	0.161	0.155	0.120	0.120
44 <i>Tarentola angustimentalis</i> DB1402	0.222	0.215	0.222	0.208	0.232	0.221	0.221	0.211	0.214	0.214
45 <i>Tarentola boehmei</i> DB241	0.223	0.219	0.223	0.216	0.229	0.219	0.219	0.216	0.210	0.210